

University of Groningen

Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird

van Gils, Jan A.; van der Geest, Matthijs; Leyrer, Jutta; Oudman, Thomas; Lok, Tamar; Onrust, Jeroen; de Fouw, Jimmy; van der Heide, Tjisse; van den Hout, Piet J.; Spaans, Bernard

Published in:

Proceedings of the Royal Society of London. Series B, Biological Sciences

DOI:

[10.1098/rspb.2013.0861](https://doi.org/10.1098/rspb.2013.0861)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2013

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van Gils, J. A., van der Geest, M., Leyrer, J., Oudman, T., Lok, T., Onrust, J., de Fouw, J., van der Heide, T., van den Hout, P. J., Spaans, B., Dekinga, A., Brugge, M., & Piersma, T. (2013). Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 280(1763), 0861-1-0861-10. [20130861]. <https://doi.org/10.1098/rspb.2013.0861>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.



Cite this article: van Gils JA, van der Geest M, Leyrer J, Oudman T, Lok T, Onrust J, de Fouw J, van der Heide T, van den Hout PJ, Spaans B, Dekinga A, Brugge M, Piersma T. 2013 Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. *Proc R Soc B* 280: 20130861.
<http://dx.doi.org/10.1098/rsob.2013.0861>

Received: 6 April 2013

Accepted: 13 May 2013

Subject Areas:

behaviour, ecology, theoretical biology

Keywords:

diet choice, hydrogen sulphide, optimal foraging theory, predator–prey interactions, survival rate, toxins

Author for correspondence:

Jan A. van Gils

e-mail: jan.van.gils@nioz.nl

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsob.2013.0861> or via <http://rsob.royalsocietypublishing.org>.

Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird

Jan A. van Gils¹, Matthijs van der Geest¹, Jutta Leyrer^{1,2,3}, Thomas Oudman¹, Tamar Lok^{1,2}, Jeroen Onrust¹, Jimmy de Fouw¹, Tjisse van der Heide⁴, Piet J. van den Hout¹, Bernard Spaans¹, Anne Dekinga¹, Maarten Brugge¹ and Theunis Piersma^{1,2}

¹Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg (Texel), The Netherlands

²Animal Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

³Centre for Integrative Ecology, Deakin University, Warrnambool Campus, Geelong, Victoria 3217, Australia

⁴Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

Recent insights suggest that predators should include (mildly) toxic prey when non-toxic food is scarce. However, the assumption that toxic prey is energetically as profitable as non-toxic prey misses the possibility that non-toxic prey have other ways to avoid being eaten, such as the formation of an indigestible armature. In that case, predators face a trade-off between avoiding toxins and minimizing indigestible ballast intake. Here, we report on the trophic interactions between a shorebird (red knot, *Calidris canutus canutus*) and its two main bivalve prey, one being mildly toxic but easily digestible, and the other being non-toxic but harder to digest. A novel toxin-based optimal diet model is developed and tested against an existing one that ignores toxin constraints on the basis of data on prey abundance, diet choice, local survival and numbers of red knots at Banc d'Arguin (Mauritania) over 8 years. Observed diet and annual survival rates closely fit the predictions of the toxin-based model, with survival and population size being highest in years when the non-toxic prey is abundant. In the 6 of 8 years when the non-toxic prey is not abundant enough to satisfy the energy requirements, red knots must rely on the toxic alternative.

1. Introduction

Toxic food is better avoided, and there is a large literature on how predators learn to avoid toxic prey [1–6]. Nevertheless, an emerging alternative view is that predators should not entirely neglect toxic prey as long as this could increase their opportunity to gain energy [7–13]. Mildly toxic prey species that are not directly lethal upon ingestion could be valuable during times when non-toxic food is in short supply [14,15]. There are a number of cases where predators have been reported to consume toxic but not-immediately-lethal prey [16–21], but the dietary choices [7,17,19–21] and subsequent demographic consequences [18] remain unexplained in mechanistic and functional terms.

Optimization models may help us to understand how predators should strategically trade off the minimization of toxin ingestion with the maximization of energy gain. Recent state-dependent models predict that the hungrier a predator is, the more likely it is to accept toxic prey [9,10], a prediction that was upheld that empirically [8,13]. Furthermore, through a predator's hunger state, the willingness to include mildly toxic prey should depend on the

abundance and availability of non-toxic food, which is a prediction that allows field testing. However, when it comes to field testing, in both the models and the experiments, the only difference between prey types was their degree of toxicity, and this may be quite unrealistic.

In nature, prey species differ in many more defence traits than degrees of toxicity. By making it difficult for a predator to detect, capture, ingest or digest prey [22,23], non-toxic and nutritious prey species may escape predation. Predators therefore need to deal with multiple constraints, and may face much steeper trade-offs between energy gain and toxin avoidance than hitherto assumed. Here, we will focus on such a system in which a predator faces the choice between an easy to digest toxic prey and a much harder to digest non-toxic prey. Building upon the existing digestive rate model (DRM) developed by Hirakawa [24], which includes a digestive constraint but not a toxin constraint, we have developed a novel toxin-digestive rate model (TDRM) to generate food-density-dependent predictions on optimal diet and maximum energy intake rates for systems where prey differ in toxicity. The predictions of both the DRM and the TDRM are then put to the test in an 8-year field study on food abundance, diet choice, survival rate and population size in a molluscivore vertebrate predator, the red knot (*Calidris canutus canutus*, hereafter knot), in its non-breeding area at Banc d'Arguin (Mauritania), characterized by a highly sulfidic environment in which the most abundant mollusc prey is toxic, while other prey types are not.

(a) Study system

The intertidal flats at Banc d'Arguin are densely covered by seagrass (mainly *Zostera noltii* Hornem.) [25]. Detritus is produced at a high rate, which is degraded anaerobically by sulphate-reducing bacteria [26], causing a build-up of high concentrations of hydrogen sulphide in sediment pore water [27,28]. Sulphide is toxic to many organisms as its lipid solubility enables it to freely penetrate biological membranes, eventually slowing down the functioning of mitochondria and the production of ATP [29]. A specialized group of organisms that can profit from high sulphide concentrations in seagrass beds are Lucinidae [30], heterodont bivalves that live in symbiosis with chemoautotrophic bacteria inside their gill structures [31]. These bacteria oxidize sulphide that is provided by the lucinid host to synthesize sugars which fuel both the growth of the lucinid host and its endosymbiotic bacteria [32]. The lucinid *Loripes lucinalis* (hereafter *Loripes*) is the dominant bivalve in Banc d'Arguin, with densities of up to 4000 individuals per m² [33,34], and hence Banc d'Arguin can be considered as a chemosynthesis-based ecosystem [35].

Banc d'Arguin is an important non-breeding area for Arctic-breeding shorebirds, hosting more than two million individuals in winter, with knots being the most abundant molluscivore [36]. Knots face a trade-off between feeding on the superabundant but toxic *Loripes* [37] and a much less abundant but non-toxic prey, *Dosinia isocardia* (hereafter *Dosinia*); numerically, *Loripes* and *Dosinia* together make up 75 per cent of all molluscs that are ingestible by knots [38,39] and dominate the diet of knots [40]. Knots face an additional trade-off: *Loripes* has a very thin shell, whereas *Dosinia* has a thicker armature. As knots ingest their prey whole [41], they often face a digestive processing constraint [42], which can be alleviated by selecting bivalves that have high flesh-to-shell mass ratios [43]. The toxicity of *Loripes*

for knots has recently been investigated experimentally [37]. Captive knots that were given a *Loripes*-only diet quickly developed diarrhoea, thereby losing significant amounts of water. Their compensatory water consumption could not prevent a decrease in food intake. When given a diet of non-toxic *Dosinia*, birds recovered within an hour. Intake rates on *Loripes* available ad libitum were three times lower than expected on the basis of maximal shell mass processing rates, whereas intake rates on *Dosinia* available ad libitum matched the prediction of a model that predicted intake as constrained by the processing of shells. When given the choice between *Dosinia* and *Loripes*, the captive birds included both prey types in their diet, which maximized their energy intake rate as predicted by a model developed for ad libitum situations.

(b) Toxin-digestive rate model

The TDRM is developed for non-ad libitum circumstances, where foragers need to search for their prey. In its most simple form, it assumes that there are just two prey types $i = 1, 2$, which can each be characterized by energy contents e_i , indigestible ballast mass k_i , toxin contents s_i , handling time h_i , searching efficiency a_i and density D_i . The problem is finding the acceptance probabilities $P = (p_1, p_2)$ for both prey types that maximize the forager's long-term energy intake rate Y . The latter is given by the multi-species version of Holling's disc equation [44]:

$$Y = \frac{p_1 a_1 D_1 e_1 + p_2 a_2 D_2 e_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2}. \quad (1.1)$$

In the 'classical prey model' [45], which ignores possible digestive and toxin constraints, finding the optimal solution is straightforward. First, rank prey types such that $e_1/h_1 > e_2/h_2$. Always accept type 1 ($p_1 = 1$), and accept type 2 ($p_2 = 1$) whenever $a_1 D_1 e_1 / (1 + a_1 D_1 h_1) \leq e_2/h_2$, otherwise reject ($p_2 = 0$). This model, called the 'contingency model' (CM) [46], has been upheld in many diet studies on a variety of foragers [47], but was refuted in the case of knots [43,48]. As knots face a digestive constraint, they should and do take a prey's ballast mass into account when selecting their diet [43].

If ballast intake rate X for the optimal solution in the CM exceeds digestive constraint c , then the forager faces a digestive bottleneck, in which case the CM yields a suboptimal solution [24]. Then, the rate-maximizing diet choice can be found using the DRM [24]. This model can be solved graphically by plotting energy intake rate Y against ballast intake rate X for all possible combinations of P , including partial preferences for either type (figure 1a). Then, by drawing digestive constraint c (vertical bar in figure 1a), one can work out which diet choice P yields the maximum sustainable energy intake rate Y under constraint c (asterisk in figure 1a). For details, we refer to the original paper by Hirakawa [24] and its first applications in knots [43], for which such an 'all-or-nothing constraint' has explained intake rate [42], prey choice [43,48], patch choice [49], selection of stopover sites [50] and even digestive organ sizes [42,51,52]. As already mentioned by Hirakawa [24], the same graphical procedure can be followed when the forager faces a toxin rather than a digestive constraint (replacing ballast intake rate X by toxin intake rate Z and ballast contents k_i by toxin contents s_i).

However, a forager's energy intake rate may be bottlenecked by both a digestive and toxin constraint. This occurs

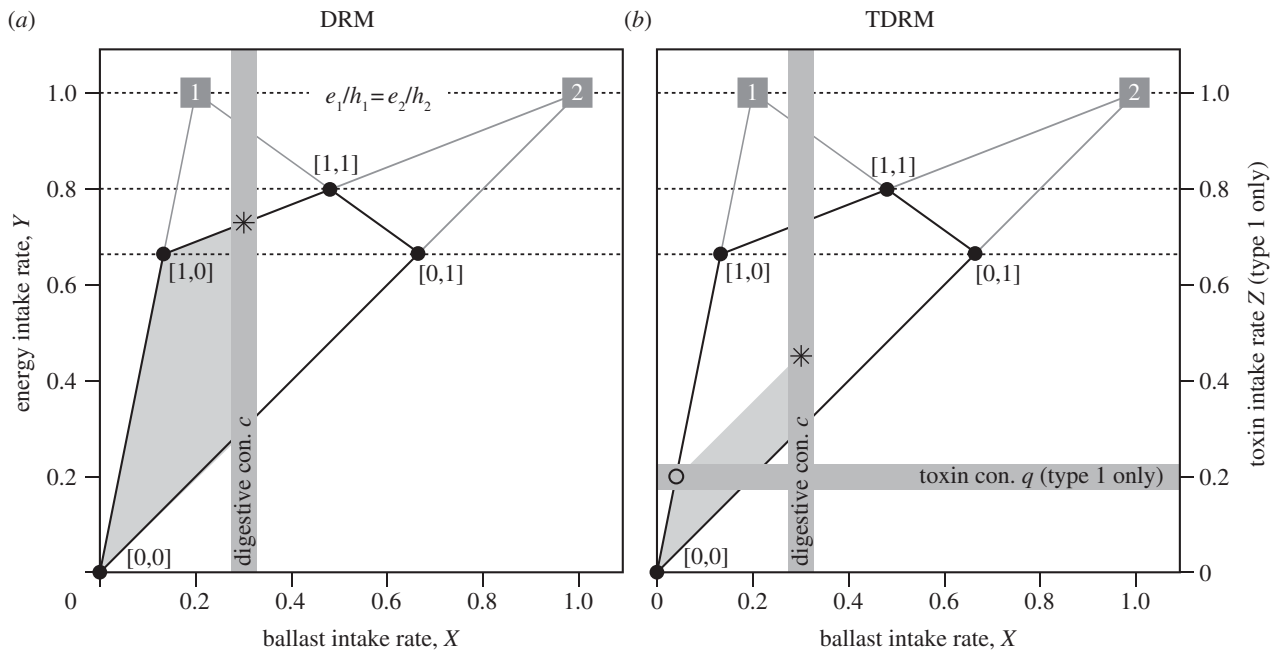


Figure 1. Graphical solution, following Hirakawa [24] and van Gils *et al.* [43], to find the optimal choice between two prey types, which maximizes energy intake rate (asterisk in both graphs) under (a) one or (b) two constraints. In both graphs, squared symbols give maximum intake rates at infinite densities of either type 1 or type 2 when there would be no constraints, kite-shaped surface bordered by black solid lines gives feasible intake rates under (given) finite prey densities, grey area within the kite shape gives feasible intake rates under the acknowledgement of (a) a digestive constraint (con.) and (b) both a digestive and a toxin constraint. Numbers in squared brackets give diet choice as $[p_1, p_2]$. (a) Accounting only for a digestive constraint, the DRM ranks prey types on the basis of digestive quality (e/k) and predicts for this case that the high-quality prey (type 1) should be fully accepted ($p_1 = 1$), whereas the poor-quality prey (type 2) should only be partially selected ($0 < p_2 < 1$). (b) Accounting for both constraints, the TDRM predicts partial preference on both prey types ($0 < p_1 < 1$ and $0 < p_2 < 1$). Maximum energy intake rate is found by drawing a line parallel to the lower line of the kite shape (this line is parallel because toxin intake rate Z is kept at q across this line), starting where toxin constraint q crosses the left-most line of the kite shape (open dot) until it hits digestive constraint c (asterisk). Note that the scenario plotted here mimics our study qualitatively (the only toxic prey is the type with the highest e/k ratio), but not quantitatively (parameter values have been chosen arbitrarily).

when, accounting for digestive constraint c in the DRM (i.e. when $X > c$ in the optimal CM solution), toxin intake rate Z in the optimal DRM solution exceeds q . This can occur only when the highest-digestive-quality prey (i.e. the one with the highest e_i/k_i) is most toxic (i.e. the one with the highest e_i/s_i ; in our *Loripes-Dosinia* case, this condition was always upheld; electronic supplementary material, table S1). Graphically, the optimal solution under both constraints can be found by adding a third axis to Hirakawa's state space (figure 1b; note that we have added the third axis to the existing two-dimensional plane, making reading the details easier; we could have also plotted X , Y and Z three-dimensionally). Solving the model analytically is equally straightforward and we will refer to it as TDRM (note that TDRM equals a DRM when only one of the two constraints operates, which in turn equals a CM when none of the constraints is present). First, maximal sustainable ballast intake rate X is set by digestive constraint c ,

$$X = c, \quad (1.2a)$$

which can be written as

$$\frac{p_1 a_1 D_1 k_1 + p_2 a_2 D_2 k_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} = c. \quad (1.2b)$$

Similarly, maximally tolerable toxin intake rate Z is set by toxin constraint q ,

$$Z = q, \quad (1.3a)$$

which can be written as

$$\frac{p_1 a_1 D_1 s_1 + p_2 a_2 D_2 s_2}{1 + p_1 a_1 D_1 h_1 + p_2 a_2 D_2 h_2} = q. \quad (1.3b)$$

Solving equations (1.2b) and (1.3b) for the two unknown variables p_1 and p_2 yields the optimal acceptance probabilities

$$p_1 = \frac{s_2 c - k_2 q}{a_1 D_1 (s_2 (k_1 - h_1 c) + s_1 (h_2 c - k_2) + q (h_1 k_2 - h_2 k_1))} \quad (1.4)$$

and

$$p_2 = \frac{k_1 q - s_1 c}{a_2 D_2 (s_2 (k_1 - h_1 c) + s_1 (h_2 c - k_2) + q (h_1 k_2 - h_2 k_1))}. \quad (1.5)$$

2. Material and methods

(a) Benthos

Our study period spans from 2003 to 2010, in which we collected 1024 benthos samples in 13 consecutive expeditions: Dec. 2003 ($n = 84$), Dec. 2004 ($n = 26$), Apr. 2005 ($n = 39$), Dec. 2005 ($n = 8$), Nov. 2006 ($n = 6$), Apr. 2007 ($n = 229$), Aug. 2007 ($n = 8$), Oct. 2007 ($n = 12$), Feb. 2008 ($n = 142$), Apr. 2008 ($n = 78$), Nov. 2008 ($n = 56$), Oct. 2009 ($n = 224$) and Oct. 2010 ($n = 112$). Following procedures described elsewhere [28,43,49], a benthos sample represented a sediment core (diameter: 15 cm) taken to a depth of 20 cm and sieved over a 1 mm sieve. Top (0–4 cm) and bottom (4–16 cm) parts of the sample were sieved separately in order to distinguish between prey that are accessible and inaccessible to

knots [53]. In the laboratory, each mollusc was identified to species level, and shell length was determined (± 0.1 mm). The latter allowed us to distinguish between ingestible and non-ingestible prey (knots can ingest all size classes of *Loripes* and *Dosinia* < 13.2 mm). By drying (3 days at 60°C), weighing (± 0.1 mg) and incinerating (5 h at 550°C) flesh and shell separately, we determined individual flesh ash-free dry mass $\text{AFDM}_{\text{flesh}}$ and shell dry mass DM_{shell} from subsamples. The relationships of $\text{AFDM}_{\text{flesh}}$ and DM_{shell} with shell length were used to predict missing values for those prey items that were not weighed. Next, numerical density (D in equations (1.1)–(1.5)), $\text{AFDM}_{\text{flesh}}$ (e in equation (1.1)) and DM_{shell} (k in equations (1.2b), (1.4), (1.5)) were averaged per year per species (available items only, i.e. those accessible and ingestible), diet models and were used to calculate available biomass densities and as input variables in the two diet models (see the electronic supplementary material, table S1; toxin contents s was equated to flesh contents e in case of *Loripes* because toxin constraint q is expressed in terms of *Loripes* flesh intake). Further parameter values used were searching efficiency $a = 4 \text{ cm}^2 \text{ s}^{-1}$ [28,54], handling time $h = 1 \text{ s}$ [28], toxin constraint $q = 0.1 \text{ mg AFDM}_{\text{flesh}} \text{ s}^{-1}$ [37] (*Loripes* only) and gizzard mass = 10 g [50], resulting in digestive constraint $c = 5 \text{ mg DM}_{\text{shell}} \text{ s}^{-1}$ [42].

All samples were taken in the vicinity (less than 5 km) of Iwik, Banc d'Arguin (19°53' N, 16°18' W). Samples collected in 2003, 2004 and 2006 were taken closer to Iwik (0–3 km) than in other years (1–5 km). Spatial differences at this scale might have had little influence. Yet smaller-scale spatial parameters such as distance to gullies, affecting the presence of seagrass [55], might have had a larger effect. *Loripes* is mostly found in seagrass, whereas *Dosinia* is almost as abundant in bare as in seagrass habitat [38], and differences in prey densities between years may thus in part be due to differences in spatial design (on average, seagrass covers 80% of the intertidal surface at Banc d'Arguin [25]). We tested potential biases for both spatial scales by comparing our 2004 data (0–3 km to Iwik) with those of an independent study also from 2004 by Honkoop *et al.* [38], who sampled mudflats 1–5 km away from Iwik and took an equal number of samples in bare and in seagrass habitat. 2004 was a notable year in which *Dosinia* was more abundant than *Loripes* (1142.7 versus 23.9 m^{-2} in our study and 216.6 versus 198.2 m^{-2} in the study by Honkoop *et al.* [38]; after correcting their stratified data for the 80% seagrass coverage of the intertidal flats and for the species-specific availability fractions, 0.73 for *Dosinia* and 0.70 for *Loripes* [28]). We repeated all analyses by replacing our 2004 benthos data by those of Honkoop *et al.* [38], which revealed that neither the outcome of the survival analyses nor the outcome of the diet comparisons was sensitive to our spatially inconsistent sampling programme (see the section on sensitivity analysis with respect to benthos sampling in the electronic supplementary material).

(b) Diet composition

During six of the 13 expeditions, we collected 77 faecal samples (2003, $n = 21$; 2004, $n = 6$; Apr. 2007, $n = 8$; Oct. 2007, $n = 14$; Feb. 2008, $n = 11$; 2009, $n = 17$), samples usually containing 40–60 droppings. Samples were sorted using standard methodology [56], which has recently been calibrated for knots feeding on *Dosinia* and *Loripes* [40]. In short, after drying (3 days at 60°C), shell fragments that were retained on a 300 μm sieve were sorted out and weighed per species, yielding species-specific estimates of ingested DM_{shell} (after correcting for 35% of DM_{shell} not being retained on the sieve [40]). Next, hinges were assorted to species and their heights were determined in order to reconstruct ingested size distributions. The latter was needed to express a species's relative diet contribution in terms of total $\text{AFDM}_{\text{flesh}}$ consumed, because $\text{AFDM}_{\text{flesh}}/\text{DM}_{\text{shell}}$ ratios are size-dependent [56]. Relative diet compositions were logit-transformed before calculating the annual averages [57].

(c) Annual survival rates

Survival estimates were based on capture/resighting data of a total of 1595 individually marked knots. The birds were captured and resighted during annual three-week expeditions in November/December 2002–2010 [58], yielding annual survival estimates for seven consecutive years (2003–2009; because survival rate cannot be separated from resighting probability for 2010 when modelled with time dependence). The birds were aged upon capture [59], distinguishing hatch-year birds (juveniles) from older birds (adults). Apparent (or local) survival (Φ) and recapture probabilities (p) were estimated from live encounter data using Cormack–Jolly–Seber models [60]. As benthos and diet data were collected throughout the entire study area, we pooled the data of the two sites in our study area, Abelgh Eiznaya and Baie d'Aouatif [58,61]. Based on knowledge gained from earlier analyses, we made some *a priori* assumptions to reduce the number of parameters in order to increase the precision of the survival estimates: it has been shown that a time-since-marking (tsm) effect explained most of the variation in annual survival [58], and we thus considered tsm effects to account for transients or handling effects on survival in the first year after capture (Φ^1) versus subsequent years (Φ^{2+}). It has further been shown that age at capture (adult versus juveniles) explained a significant part of the variation in survival [58], and we thus included age at capture in our models. Note that knots were treated as adults after their first year (more than 12 months of age), and consequently no age differences existed within the Φ^{2+} category. As we were interested in which of the two diet models best explained the annual variation in survival rate, we included intake rates predicted by the TDRM and DRM, respectively, as continuous variables in the models. Additionally, to test for survival differences among years, we included time as a factor (time), but also tested whether there was a linear trend in survival rate over time (Time), because an earlier analysis indicated a decline in knot survival over time [62]. In all models, resighting probability p was modelled as a function of time (again as a factor) and site, as observation effort differed between the two sites, and logistic improvements suggested resighting efforts differed between years [58]. Both adults and juveniles forage on open mudflats during low tide and assemble at roosts during high tide, and we had no reason to expect p to differ between age classes.

The global model was $\Phi_{\text{age} \times \text{tsm} + \text{time}} p_{\text{site} + \text{time}}$ and we tested the goodness of fit using the median- \hat{c} (c-hat) test implemented in the MARK software v. 6.0 [63]. The level of overdispersion was estimated at $\hat{c} = 1.05 \pm 0$. Models were constructed and run in R (v. 2.15.0) using the RMARK v. 2.1.4 package [64] as an interface for program MARK [63]. We used model averaging to calculate survival and resighting probability, and present parameter estimates as $\hat{\theta} \pm 1$ s.e. Model selection was based on Akaike's information criterion corrected for small sample size and overdispersion (\hat{c} ; QAIC_c). Based on the earlier-mentioned assumptions, the candidate model set consisted of all biologically and ecologically plausible combinations of parametrizations for Φ and p (see the electronic supplementary material, table S2).

(d) Estimating and predicting population dynamics

Each year between 2002 and 2010, we carried out a single count of all knots roosting in the Iwik study region. This took place during a daytime spring high tide in November/December. Birds were counted using telescopes by four or five teams of two observers, each counting a subsection of our study area.

We modelled the population trend for 2002–2010 using adult and juvenile survival rates estimated by the most parsimonious model (i.e. survival model 1 in electronic supplementary material, table S2). In this statistical model, TDRM energy

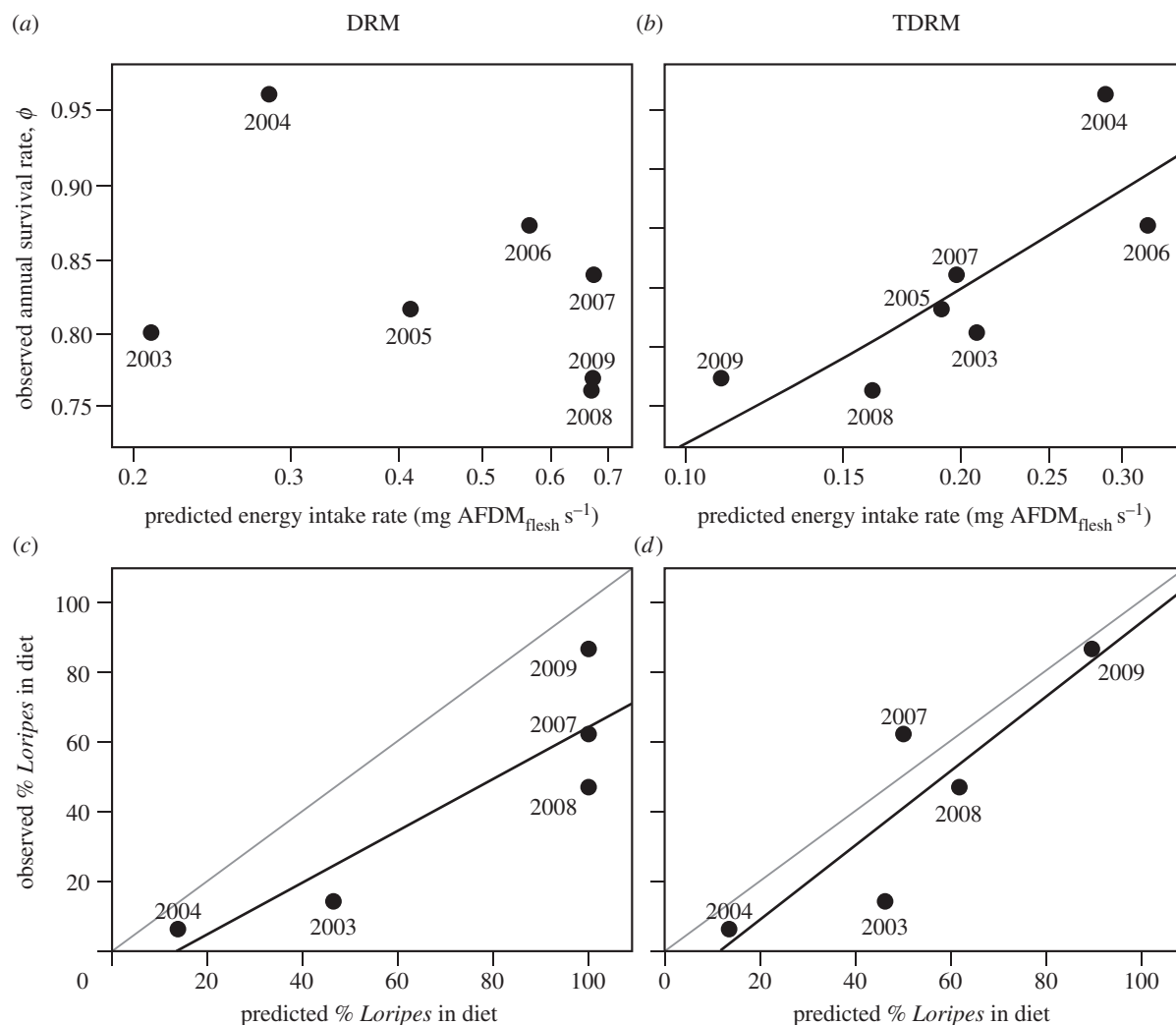


Figure 2. (a) Year-specific adult survival rate (estimated by model 2 in electronic supplementary material, table S2; year runs from Nov/Dec of the previous year to Nov/Dec of the plotted year) does not correlate with the DRM-predicted intake rate, (b) whereas it correlates positively with the intake rate predicted by the TDRM. Line gives model fit (model 1 in electronic supplementary material, table S2). (c) Observed amounts of *Loripes* in the diet (relative to *Dosinia*) are lower than predicted by the DRM, (d) but match with TDRM-predictions. Grey lines represent $y = x$ lines, and black lines are significant regression lines.

intake rates Y served as input, which were predicted on the basis of equation (1.1) using (i) the observed densities of both *Loripes* and *Dosinia*, (ii) the observed densities of *Loripes* only, and (iii) the observed densities of *Dosinia* only. The last two hypothetical scenarios allow us to hypothesize how much knot population dynamics depend on the presence of either *Loripes* or *Dosinia*. As applied before when modelling knot population dynamics [65], we used a two-dimensional matrix population model, in which fecundity (f ; equal to 0 for juveniles and 0.14 yr^{-1} for adults [66]), juvenile survival (Φ_{juv}) and adult survival (Φ_{ad}) determine how the number of juveniles (N_{juv}) and adults (N_{ad}) in year t affect the number of juveniles and adults in year $t + 1$:

$$\begin{bmatrix} N_{\text{juv}} \\ N_{\text{ad}} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & f \\ \Phi_{\text{juv}} & \Phi_{\text{ad}} \end{bmatrix}_t \begin{bmatrix} N_{\text{juv}} \\ N_{\text{ad}} \end{bmatrix}_t. \quad (2.1)$$

The 2002 count was used as the initial population size in the model.

3. Results

(a) Annual survival rate

TDRM models were substantially better supported than models including DRM intake rates (cumulative QAIC_c

weight: 0.38 for models including TDRM intake rates, and 0.00 for models including DRM intake rates; electronic supplementary material, table S2; figure 2a,b). Although models including annual variation as explanatory factor (i.e. factor time) scored high in the model selection process (cumulative QAIC_c weight: 0.48; electronic supplementary material, table S2), they added extra parameters (complexity) to the models and should thus be less favoured. There was no evidence for a time trend in survival (i.e. models including Time; cumulative QAIC_c weight: 0.14; electronic supplementary material, table S2). Furthermore, there was no support for adult survival being different in the first year after marking, compared with subsequent years (model 2 versus model 3, $\Delta\text{QAIC}_c = 0.34$). Model-averaged survival estimates can be found in the electronic supplementary material, table S3.

(b) Diet composition

The observed contribution of *Loripes* to the diet was less than predicted by the DRM (figure 2c; $t = -3.44$, d.f. = 4, $p = 0.03$). For 3 of 5 years for which we had diet data available, the DRM predicted that knots should fully ignore *Dosinia* (figure 2c). In those three years (2007, 2008, 2009), the abundance of *Loripes* was so high that, even if knots would feed

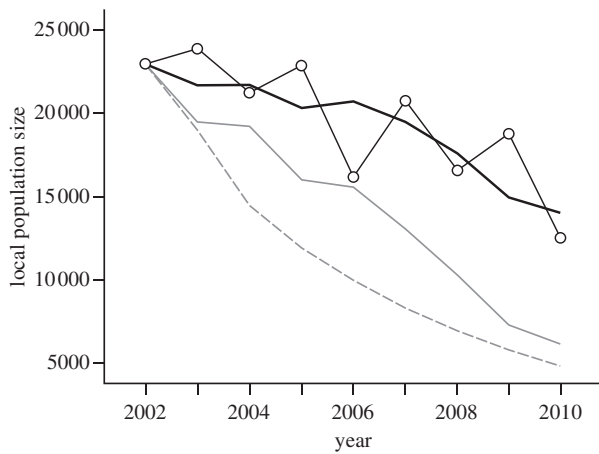


Figure 3. Predicted population dynamics of knots in the presence of both prey (thick black line), in the absence of *Loripes* (solid grey line) and in the absence of *Dosinia* (dashed grey line). Observed population size (circles connected by thin black line) follows predicted population decline based on both prey.

on *Loripes* only—the prey with the highest flesh-to-shell mass ratio—their gizzard would not be able to achieve the required shell mass processing rate (i.e. knots would face a digestive constraint). Hence, only a proportion of encountered *Loripes* should have been accepted (see the electronic supplementary material, table S4; note that this is different from conceptual figure 1a where, for reasons of visual clarity, we assumed that even maximum ballast intake rates on prey type 1, i.e. k_1/h_1 , are below digestive constraint c).

By contrast, diet compositions predicted by TDRM matched the observed diets (figure 2d; $t = -1.26$, d.f. = 4, $p = 0.28$). In 3 of 5 years, the intake rate on *Loripes* would have exceeded the toxin constraint if all encountered *Loripes* were accepted. Hence, only a proportion of the encountered *Loripes* should have been accepted for this reason (see the electronic supplementary material, table S4). In those years, knots following the TDRM could accept all encountered (ingestible) *Dosinia* as the occurrence of the toxin constraint kept shell mass processing rates low, and thereby prevented a digestive constraint. Only in the year that *Loripes* was less abundant than *Dosinia* (2004) does the TDRM predict a digestive rather than a toxin constraint. In 2004, knots should thus have accepted all encountered *Loripes* and only a fraction of the encountered (ingestible) *Dosinia* (see the electronic supplementary material, table S4).

(c) Predicted and observed population dynamics

Predicted knot population size declined over time, with the decline being steepest if *Dosinia* would have been removed from the system (−79% from 2002 to 2010), followed by the scenario when *Loripes* would have been removed (−74%). However, even with both prey included in the diet, knot numbers were predicted to decrease over time (−39%; figure 3). This last model agreed best with the observed decline in knot numbers from 22 859 in 2002 to 12 465 in 2010 (−45%; figure 3).

4. Discussion

Knot annual survival rates correlated strongly with annual variations in *Dosinia* abundance (figure 4a; Pearson's

$r = 0.91$), but showed no trend with *Loripes* abundance (figure 4b; Pearson's $r = -0.72$). This strongly suggests that knots need non-toxic *Dosinia* to survive and cannot rely on *Loripes* only, even though *Loripes* is much more abundant and has a much higher flesh-to-shell ratio. The reasoning for this dependency is rather simple: in order to prevent lethal intoxication, knots can ingest *Loripes* up to a rate that is only half of their required intake rate [37], and they need prey such as *Dosinia* to meet their energy demands. On the other hand, *Dosinia* was not abundant enough for knots to fully rely on them as an energy source.

The TDRM, which seems to capture the essence of the knots' dietary problem, assumes the following strategy: accept toxic but energy-rich *Loripes* until toxin constraint is met, then add bulky *Dosinia* until the digestive constraint is met. According to our calculations, knots faced both constraints only in 2006, when both prey species occurred in high densities (figure 4c; for detailed calculations, see the electronic supplementary material, 'figure 4c explained'). In most years (six of eight; figure 4c), however, *Dosinia* was not abundant enough for the birds to become digestively constrained, whereas the presence of *Loripes* was usually high enough to meet the toxin constraint (figure 4c). This explains the negative correlation between the relative amount of *Loripes* in the diet and the available density of *Dosinia* (figure 5a): although the absolute rate at which *Loripes* was eaten was likely to be constant each year (equal to toxin constraint q), the absolute rate at which *Dosinia* was eaten increased with the available *Dosinia* density as long as birds were not digestively constrained (this would occur at a *Dosinia* density of $0.6\text{--}0.7 \text{ g AFDM}_{\text{flesh}} \text{ m}^{-2}$). A recent study showing year-round changes in *Dosinia* and *Loripes* densities also suggests that the relative contribution of *Loripes* to the diet of knots increased as *Dosinia* stocks became depleted throughout winter [39].

In Banc d'Arguin, knots need an average energy intake rate of approximately $0.2 \text{ mg AFDM}_{\text{flesh}} \text{ s}^{-1}$ in order to maintain body mass [67]. In most years, knots would only achieve half of this rate only if they would fully neglect *Loripes* and only accept *Dosinia* as their prey. By adding *Loripes* to their diet, knots would just meet their required energy demand. A plot of the predicted intake rate with (grey band in figure 5b) and without (dashed line in figure 5b) *Loripes* against the available *Dosinia* densities shows that energy intake rate without accepting *Loripes* would be insufficient for subsistence in 6 of 8 years (also see electronic supplementary material, table S4). Only in 2004 and 2006 would knots have been able to achieve their minimum energetic requirements on *Dosinia* alone (see the electronic supplementary material, table S4; although we modelled knots as 'intake rate maximizers', they could just as well have featured as 'sulphide minimizers' in these 2 years by fully ignoring *Loripes*; however, the diet data available for 2004 suggest they did not; figure 5a).

Note that rate maximization while feeding allows for the minimization of daily feeding time if a fixed amount of daily energy is required [68]. Minimizing daily feeding time can be beneficial if foraging comes at a cost, such as for example enhanced predation risk [69]. This justifies our approach to analyse survival as a continuous function of intake rate rather than as a simple step function of whether metabolic demands are met. Note further that in poor *Dosinia* years, notably in 2009 (see figure 5b; electronic supplementary material, table S4), knots would not even have been able to survive on the combination of *Loripes* and *Dosinia* alone, and

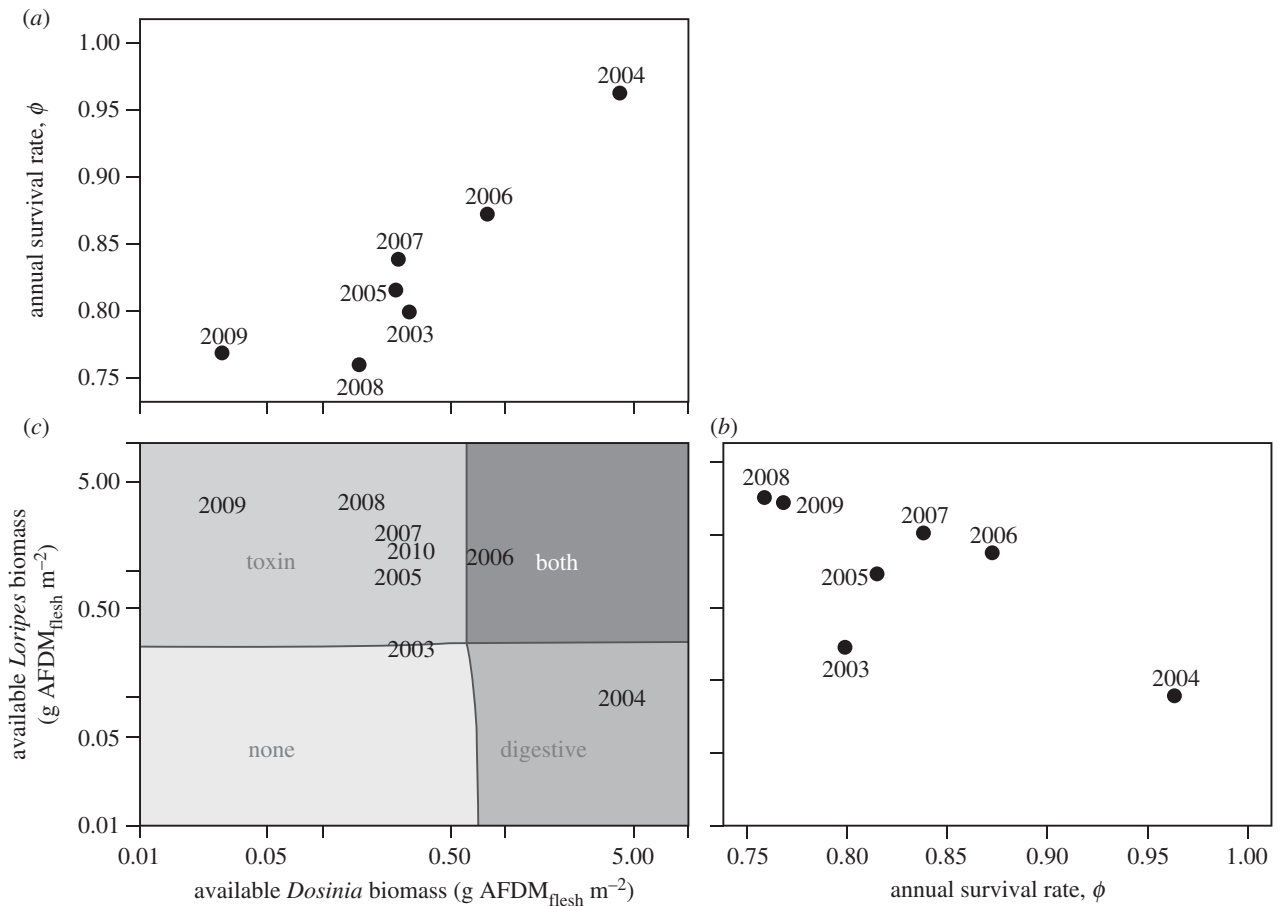


Figure 4. (a) Year-specific adult survival rate (estimated by model 2 in the electronic supplementary material, table S2) correlates with the available biomass density of *Dosinia*, (b) but not with *Loripes* density. (c) These prey densities themselves correlate negatively. Grey shading in the background indicates whether knots would face a toxin constraint, a digestive constraint, both constraints or neither. For details behind these calculations, see the electronic supplementary material, 'figure 4c explained'.

would have needed to include other prey types in their diet (which knots indeed did, especially in 2009 [40]).

With *Loripes* and *Dosinia* being by far the most abundant available bivalves at Banc d'Arguin [38], there are not many alternative mollusc prey types to include in the diet. This notion, and the fact that the last years of our study period have not shown high densities of *Dosinia* (figure 4c), may explain why the local knot population has declined during especially the second half of our study period (figure 3). However, TDRM energy intake rate showed no trend over time ($r = 0.51$, $F_{1,6} = 2.07$, $p = 0.20$). In addition, also in 1980s, when knot numbers were 40–50 per cent times higher than nowadays [70], *Dosinia* and other non-toxic alternatives were never very abundant [71]. Being a migratory species, it may thus very well be that the carrying capacity of the population is set elsewhere outside Banc d'Arguin [67]; for example, in the Wadden Sea southward staging area, where commercial fisheries led to impaired (re)fuelling opportunities [72].

It is yet unclear what determines the probability of high densities of *Dosinia*, but the negative correlation between annual averages of *Dosinia* and *Loripes* densities is remarkable (figure 4c; $r = -0.76$, $F_{1,6} = 8.30$, $p = 0.03$). As has been suggested elsewhere [28], this indicates some form of competition between the two species. Alternatively, there may be differences in environmental conditions among years that steer the negative correlation. For example, observed dynamics in seagrass abundance may underlie this correlation [55,58], with *Loripes* more strongly linked to seagrass habitat than *Dosinia* [38].

It is exciting to hypothesize about how defence strategies in one prey may have been selected for given the defence strategy in another prey. For example, is the bulkiness of *Dosinia* an evolutionary response to the toxicity of *Loripes*? The comparison between the DRM and the TDRM allows us to hypothesize along these lines: it suggests that toxicity of *Loripes* might have increased predation pressure on *Dosinia*, inducing, on an evolutionary time scale, extra armature in *Dosinia*. The reason behind this is that intake rates on *Dosinia* are much higher in the TDRM than in the DRM, especially in years of high *Loripes* abundance (see the electronic supplementary material, table S4). Under the DRM, which treats *Loripes* as if it was non-toxic, knots can reach their digestive constraint on *Loripes* only, leaving no room to add bulky *Dosinia*. By contrast, under the TDRM, many *Dosinia* can be added to the diet because intake rates on *Loripes* are reduced because of the toxicity constraint.

At the same time, the evolution of thick-shelled armature in *Dosinia* may have led to increased predation pressure on *Loripes*, which in turn may have increased *Loripes*'s toxicity. Namely, if *Dosinia* had been relatively thinner shelled than *Loripes* (i.e. when $e_D/k_D > e_L/k_L$), then knots would prefer *Dosinia* over *Loripes* and would fully neglect *Loripes* in *Dosinia*-rich years. Note that the mechanism of enhanced predation pressure on one prey type as a consequence of induced anti-predator defence in the other prey type proposed here is a classic example of 'trait-mediated indirect interactions', which have received renewed attention in the ecological literature [73–75].

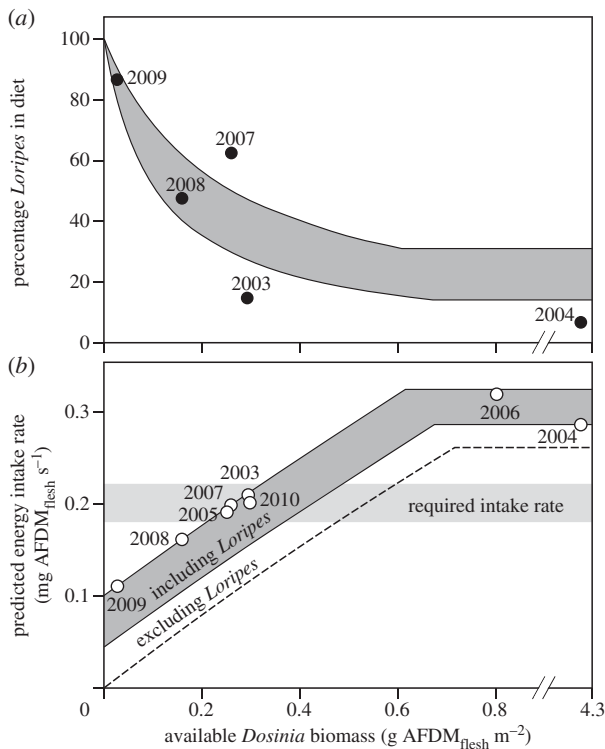


Figure 5. (a) How the amount of *Loripes* in the diet (relative to *Dosinia*) relates to the available density of *Dosinia*, both theoretically (TDRM) and empirically. Theoretical predictions are given by the grey band, with lower line representing a poor *Loripes* density ($0.1 \text{ g AFDM m}^{-2}$) and upper line a higher *Loripes* density ($\geq 0.25 \text{ g AFDM m}^{-2}$; as knots face a toxin constraint at *Loripes* densities of at least 0.25 g m^{-2} , diet composition becomes independent of *Loripes* abundance above such densities). Diet composition becomes independent of *Dosinia* density when the digestive constraint is met (i.e. above *Dosinia* densities of $0.6\text{--}0.7 \text{ g m}^{-2}$). (b) TDRM functional response to variations in *Dosinia* density. Grey band as in (a) shows that most variation in intake rate is due to density variations in *Dosinia* rather than in *Loripes*. Nevertheless, without *Loripes*, intake rates would be substantially lower (dashed line) and often below the level required for subsistence. Dots denote year-specific predictions based on *Loripes* and *Dosinia* densities.

With the chemoautotrophically fuelled *Loripes* being the top most abundant bivalve in the system, Banc d'Arguin can be classified as a chemosynthesis-based ecosystem [35]. In contrast

to Banc d'Arguin, most chemosynthesis-based ecosystems, such as deep-sea vents and seep systems, are renowned for their lack of predators [19,76,77]. Possibly, such systems lack predators because of the overwhelming densities of toxic prey, whereas non-toxic alternatives are not at hand [78]. The presence of a suitable non-toxic prey may explain why predators are able to thrive at Banc d'Arguin. Hydrothermal vents and deep-sea cold seeps are geographically more isolated than seagrass beds, and also more hostile because of the limited availability of dissolved oxygen in the deep sea. Their isolated positions make it costly for predators to switch between 'phototrophic' and 'chemotrophic' prey, which could be the reason that such systems are frequented little by predators originating from photosynthetic communities [77,79,80]. By contrast, in seagrass beds, the difference between the anaerobic sulphidic and the aerobic non-toxic environment is just a matter of metres in a horizontal direction (bare versus seagrass mosaics [38,81]), or even centimetres when considered vertically (sulphide concentrations strongly increase in the first 12 cm of the sediment layer [28]). This allows predators to 'make the best of both worlds' by adding toxic prey to their non-toxic diet as long as toxin levels do not exceed a given threshold. This mimics the problems recognized long ago for terrestrial herbivores, in which diet selection [82,83], habitat use [84], and fitness and population processes [85] are governed by the occurrence of toxins in the form of secondary plant metabolites or as products from endosymbiotic relationships [86,87]. Our work seems to be the first to make similar problems apparent in a system with predators and prey rather than herbivores and plants.

We are grateful to Parc National du Banc d'Arguin (PNBA) for their permission to work in the park and for using their facilities. The local crew at Iwik, most notably Amadou Abderahmane Sall, Sidi Ely, Mohammed Camara and Lemhaba Ould Yarba, helped in many different ways, while Brecht De Meulenaer, Joop van Eerbeek, Eelke Folmer, Erik Jansen, Han Olff, Erik Rosendaal and Hanneke Gillis assisted in collecting and processing benthos samples. The last two named also analysed dropping samples. About 40 volunteers from 10 different countries helped with catching and resighting knots. Carlos Martínez del Río and two anonymous referees commented on a draft, and Dick Visser polished the figures. This work was supported by operating funds from NIOZ, and by grants from Schure-Beijerinck-Popping Fonds to J.L., the Prins Bernhard Cultuurfondsprijs voor Natuurbehoud to T.P., a MAVA-grant (Switzerland) to T.P., an NWO-WOTRO Integrated Programme (grant no. W.01.65.221.00) to T.P. and an NWO-VIDI grant (no. 864.09.002) to J.A.v.G.

References

- Alatalo RV, Mappes J. 1996 Tracking the evolution of warning signals. *Nature* **382**, 708–710. (doi:10.1038/382708a0)
- Endler JA, Mappes J. 2004 Predator mixes and the conspicuousness of aposematic signals. *Am. Nat.* **163**, 532–547. (doi:10.1086/382662)
- Gittleman JL, Harvey PH. 1980 Why are distasteful prey not cryptic? *Nature* **286**, 149–150. (doi:10.1038/286149a0)
- Greenlees MJ, Phillips BL, Shine R. 2010 Adjusting to a toxic invader: native Australian frogs learn not to prey on cane toads. *Behav. Ecol.* **21**, 966–971. (doi:10.1093/beheco/arq095)
- Halpin CG, Rowe C. 2010 Taste-rejection behaviour by predators can promote variability in prey defences. *Biol. Lett.* **6**, 617–619. (doi:10.1098/rsbl.2010.0153)
- Speed MP. 2000 Warning signals, receiver psychology and predator memory. *Anim. Behav.* **60**, 269–278. (doi:10.1006/anbe.2000.1430)
- Skelhorn J, Rowe C. 2010 Birds learn to use distastefulness as a signal of toxicity. *Proc. R. Soc. B* **277**, 1729–1734. (doi:10.1098/rspb.2009.2092)
- Barnett CA, Bateson M, Rowe C. 2007 State-dependent decision making: educated predators strategically trade off the costs and benefits of consuming aposematic prey. *Behav. Ecol.* **18**, 645–651. (doi:10.1093/beheco/arm027)
- Sherratt TN. 2003 State-dependent risk-taking by predators in systems with defended prey. *Oikos* **103**, 93–100. (doi:10.1034/j.1600-0706.2003.12576.x)
- Sherratt TN, Speed MP, Ruxton GD. 2004 Natural selection on unpalatable species imposed by state-dependent foraging behaviour. *J. Theor. Biol.* **228**, 217–226. (doi:10.1016/j.jtbi.2003.12.009)
- Skelhorn J, Rowe C. 2007 Predators' toxin burdens influence their strategic decisions to eat toxic prey. *Curr. Biol.* **17**, 1479–1483. (doi:10.1016/j.cub.2007.07.064)
- Speed MP. 1993 When is mimicry good for predators? *Anim. Behav.* **46**, 1246–1248. (doi:10.1006/anbe.1993.1321)
- Barnett CA, Skelhorn J, Bateson M, Rowe C. 2012 Educated predators make strategic decisions to

- eat defended prey according to their toxin content. *Behav. Ecol.* **23**, 418–424. (doi:10.1093/beheco/arr206)
14. Kokko H, Mappes J, Lindström L. 2003 Alternative prey can change model-mimic dynamics between parasitism and mutualism. *Ecol. Lett.* **6**, 1068–1076. (doi:10.1046/j.1461-0248.2003.00532.x)
 15. Lindström L, Alatalo RV, Lyytinen A, Mappes J. 2001 Strong antiapostatic selection against novel rare aposematic prey. *Proc. Natl Acad. Sci. USA* **98**, 9181–9184. (doi:10.1073/pnas.161071598)
 16. Williams B, Lovenburg V, Huffard C, Caldwell R. 2011 Chemical defense in pelagic octopus paralarvae: tetrodotoxin alone does not protect individual paralarvae of the greater blue-ringed octopus (*Hapalochlaena lunulata*) from common reef predators. *Chemoecology* **21**, 131–141. (doi:10.1007/s00049-011-0075-5)
 17. Beckmann C, Shine R. 2011 Toad's tongue for breakfast: exploitation of a novel prey type, the invasive cane toad, by scavenging raptors in tropical Australia. *Biol. Invasions* **13**, 1447–1455. (doi:10.1007/s10530-010-9903-8)
 18. Garcia R, Sulkin S, Lopez M. 2011 Effects on larval crabs of exposure to algal toxin via ingestion of heterotrophic prey. *Mar. Biol.* **158**, 451–460. (doi:10.1007/s00227-010-1572-8)
 19. Kicklighter CE, Fisher CR, Hay ME. 2004 Chemical defense of hydrothermal vent and hydrocarbon seep organisms: a preliminary assessment using shallow-water consumers. *Mar. Ecol. Prog. Ser.* **275**, 11–19. (doi:10.3354/meps275011)
 20. Lincango MP, Causton CE, Alvarez CC, Jimenez-Uzcategui G. 2011 Evaluating the safety of *Rodolia cardinalis* to two species of Galapagos finch; *Camarhynchus parvulus* and *Geospiza fuliginosa*. *Biol. Control* **56**, 145–149. (doi:10.1016/j.biocontrol.2010.10.006)
 21. Gray HM, Kaiser H, Green DM. 2010 Does alkaloid sequestration protect the green poison frog, *Dendrobates auratus*, from predator attacks? *Salamandra* **46**, 235–238.
 22. Caro T. 2005 *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.
 23. Jeschke JM, Tollrian R. 2000 Density-dependent effects of prey defences. *Oecologia* **123**, 391–396. (doi:10.1007/s004420051026)
 24. Hirakawa H. 1995 Diet optimization with a nutrient or toxin constraint. *Theor. Popul. Biol.* **47**, 331–346. (doi:10.1006/tpbi.1995.1015)
 25. Wolff WJ, Smit C. 1990 The Banc d'Arguin, Mauritania, as an environment for coastal birds. *Ardea* **78**, 17–38.
 26. Jørgensen BB. 1982 Mineralization of organic matter in the sea bed: the role of sulphate reduction. *Nature* **296**, 643–645. (doi:10.1038/296643a0)
 27. Calleja ML, Marbà N, Duarte CM. 2007 The relationship between seagrass (*Posidonia oceanica*) decline and sulfide porewater concentration in carbonate sediments. *Estuar. Coast. Shelf Sci.* **73**, 583–588. (doi:10.1016/j.ecss.2007.02.016)
 28. van Gils JA, van der Geest M, Jansen EJ, Govers LL, de Fouw J, Piersma T. 2012 Trophic cascade induced by molluscivore predator alters pore-water biogeochemistry via competitive release of prey. *Ecology* **93**, 1143–1152. (doi:10.1890/11-1282.1)
 29. Bagarinao T. 1992 Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organisms. *Aquat. Toxicol.* **24**, 21–62. (doi:10.1016/0166-445X(92)90015-F)
 30. Taylor JD, Glover EA, Smith L, Dyal P, Williams ST. 2011 Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). *Zool. J. Linn. Soc.* **163**, 15–49.
 31. Taylor JD, Glover EA. 2006 Lucinidae (Bivalvia): the most diverse group of chemosymbiotic molluscs. *Zool. J. Linn. Soc.* **148**, 421–438. (doi:10.1111/j.1096-3642.2006.00261.x)
 32. Johnson M, Diouris M, Le Pennec M. 1994 Endosymbiotic bacterial contribution in the carbon nutrition of *Loripes lucinalis* (Mollusca: Bivalvia). *Symbiosis* **17**, 1–13.
 33. van der Heide T *et al.* 2012 A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science* **336**, 1432–1434. (doi:10.1126/science.1219973)
 34. van der Geest M, van Gils JA, van der Meer J, Olf H, Piersma T. 2011 Suitability of calcein as an in situ growth marker in burrowing bivalves. *J. Exp. Mar. Biol. Ecol.* **399**, 1–7. (doi:10.1016/j.jembe.2011.01.003)
 35. Dubilier N, Bergin C, Lott C. 2008 Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nat. Rev. Microbiol.* **6**, 725–740. (doi:10.1038/nrmicro1992)
 36. Altenburg W, Engelmoer M, Mes R, Piersma T. 1982 *Wintering Waders on the Banc d'Arguin, Mauritania. Report of the Netherlands Ornithological Expedition 1980*. Leiden, The Netherlands: Stichting Veth tot steun aan Waddenonderzoek.
 37. Oudman T, Onrust J, de Fouw J, Spaans B, Piersma T, van Gils JA. In preparation. Toxin and digestive constraint explain partial preferences of an energy maximizing predator.
 38. Honkoop PJC, Berghuis EM, Holthuijsen S, Lavaleye MSS, Piersma T. 2008 Molluscan assemblages of seagrass-covered and bare intertidal flats on the Banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter. *J. Sea Res.* **60**, 255–263. (doi:10.1016/j.seares.2008.07.005)
 39. Ahmedou Salem MV, van der Geest M, Piersma T, Saoud Y, van Gils JA. Submitted. Seasonal changes in mollusc abundance in a tropical intertidal ecosystem, Banc d'Arguin (Mauritania): a test of the 'shorebird depletion' hypothesis.
 40. Onrust J, de Fouw J, Oudman T, van der Geest M, Piersma T, van Gils JA. In press. Red Knot diet reconstruction revisited: context dependence revealed by experiments at Banc d'Arguin, Mauritania. *Bird Study*.
 41. Piersma T, Koolhaas A, Dekinga A. 1993 Interactions between stomach structure and diet choice in shorebirds. *Auk* **110**, 552–564. (doi:10.2307/4088419)
 42. van Gils JA, Piersma T, Dekinga A, Dietz MW. 2003 Cost-benefit analysis of mollusc-eating in a shorebird. II. Optimizing gizzard size in the face of seasonal demands. *J. Exp. Biol.* **206**, 3369–3380. (doi:10.1242/jeb.00546)
 43. van Gils JA, de Rooij SR, van Belle J, van der Meer J, Dekinga A, Piersma T, Drent R. 2005 Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. *J. Anim. Ecol.* **74**, 105–119. (doi:10.1111/j.1365-2656.2004.00903.x)
 44. Holling CS. 1959 Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385–398. (doi:10.4039/Ent91385-7)
 45. Stephens DW, Krebs JR. 1986 *Foraging theory*. Princeton, NJ: Princeton University Press.
 46. Belovsky GE. 1984 Herbivore optimal foraging: a comparative test of 3 models. *Am. Nat.* **124**, 97–115. (doi:10.1086/284254)
 47. Sih A, Christensen B. 2001 Optimal diet theory: when does it work, and when and why does it fail? *Anim. Behav.* **61**, 379–390. (doi:10.1006/anbe.2000.1592)
 48. Quaintenne G, van Gils JA, Bocher P, Dekinga A, Piersma T. 2010 Diet selection in a molluscivore shorebird across Western Europe: does it show short- or long-term intake rate-maximization? *J. Anim. Ecol.* **79**, 53–62. (doi:10.1111/j.1365-2656.2009.01608.x)
 49. van Gils JA, Dekinga A, Spaans B, Vahl WK, Piersma T. 2005 Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. *J. Anim. Ecol.* **74**, 120–130. (doi:10.1111/j.1365-2656.2004.00904.x)
 50. van Gils JA, Battley PF, Piersma T, Drent R. 2005 Reinterpretation of gizzard sizes of red knots worldwide emphasises overriding importance of prey quality at migratory stopover sites. *Proc. R. Soc. B* **272**, 2609–2618. (doi:10.1098/rspb.2005.3245)
 51. van Gils JA, Piersma T, Dekinga A, Battley PF. 2006 Modelling phenotypic flexibility: an optimality analysis of gizzard size in red knots (*Calidris canutus*). *Ardea* **94**, 409–420.
 52. van Gils JA, Dekinga A, van den Hout PJ, Spaans B, Piersma T. 2007 Digestive organ size and behavior of red knots (*Calidris canutus*) indicate the quality of their benthic food stocks. *Isr. J. Ecol. Evol.* **53**, 329–346. (doi:10.1560/IJEE.53.3.329)
 53. Zwarts L, Blomert A-M, Wanink JH. 1992 Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. *Mar. Ecol. Prog. Ser.* **83**, 129–139. (doi:10.3354/meps083129)
 54. Piersma T, van Gils J, de Goeij P, van der Meer J. 1995 Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *J. Anim. Ecol.* **64**, 493–504. (doi:10.2307/5652)
 55. Folmer EO, van der Geest M, Jansen E, Olf H, Anderson TM, Piersma T, van Gils JA. 2012 Seagrass-sediment feedback: an exploration using a non-recursive structural equation model. *Ecosystems* **15**, 1380–1393. (doi:10.1007/s10021-012-9591-6)

56. Dekinga A, Piersma T. 1993 Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*. *Bird Study* **40**, 144–156. (doi:10.1080/00063659309477140)
57. Warton DI, Hui FK. 2011 The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**, 3–10. (doi:10.1890/10-0340.1)
58. Leyrer J, Lok T, Brugge M, Dekinga A, Spaans B, van Gils JA, Sandercock BK, Piersma T. 2012 Small-scale demographic structure suggests preemptive behavior in a flocking shorebird. *Behav. Ecol.* **23**, 1226–1233. (doi:10.1093/beheco/ars106)
59. Prater AJ, Merchant JH, Vuorinen J. 1977 *Guide to the identification and ageing of holarctic shorebirds*. Tring, UK: BTO.
60. Lebreton J-D, Burnham KP, Clobert J, Anderson DR. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118. (doi:10.2307/2937171)
61. Leyrer J, Spaans B, Camara M, Piersma T. 2006 Small home ranges and high site fidelity in red knots (*Calidris c. canutus*) wintering on the Banc d'Arguin, Mauritania. *J. Ornithol.* **147**, 376–384. (doi:10.1007/s10336-005-0030-8)
62. Leyrer J, Lok T, Brugge M, Spaans B, Sandercock BK, Piersma T. In press. Mortality within the annual cycle: seasonal survival patterns in Afro-Siberian red knots. *J. Ornithol.*
63. White GC, Burnham KP. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139. (doi:10.1080/00063659909477239)
64. Laake J, with contributions from E. Rakhimberdiev, B. Augustine. 2012 Package 'RMark': R code for MARK analysis, v. 2.1.4. See <http://cran.r-project.org/web/packages/RMark/RMark.pdf>.
65. Baker AJ *et al.* 2004 Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proc. R. Soc. Lond. B* **271**, 875–882. (doi:10.1098/rspb.2003.2663)
66. van den Hout PJ, van Gils JA, Robin F, van der Geest M, Dekinga A, Piersma T. In preparation. Cryptic interference forces juvenile red knots to forage longer in a dangerous environment.
67. van Gils JA, van der Geest M, Kraan C, Folmer EO, Jansen EJ, Piersma T. 2009 How the carrying capacity of the Wadden Sea regulates the number of wintering waders at Banc d'Arguin. *Limosa* **82**, 134–140.
68. Schoener TW. 1971 Theory of feeding strategies. *Annu. Rev. Ecol. Evol. S* **2**, 369–404. (doi:10.1146/annurev.es.02.110171.002101)
69. McNamara JM, Houston AI. 1994 The effect of a change in foraging options on intake rate and predation rate. *Am. Nat.* **144**, 978–1000. (doi:10.1086/285721)
70. Hagemerij W, Smit C, de Boer P, van Dijk A, Ravenscroft N, van Roomen M, Wright M. 2004 Wader and waterbird at the Banc d'Arguin, Mauritania, January 2000. In *WIWO Report 81*. Beek-Ubbergen, The Netherlands: Foundation Working Group International Waterbird and Wetland Research (WIWO).
71. Wolff WJ, Duiven AG, Duiven P, Esselink P, Gueye A, Meijboom A, Moerland G, Zegers J. 1993 Biomass of macrobenthic tidal flat fauna of the Banc d'Arguin, Mauritania. *Hydrobiologia* **258**, 151–163. (doi:10.1007/BF00006193)
72. Kraan C, van Gils JA, Spaans B, Dekinga A, Piersma T. 2010 Why Afro-Siberian red knots *Calidris canutus* have stopped staging in the western Dutch Wadden Sea during southward migration. *Ardea* **98**, 155–160. (doi:10.5253/078.098.0204)
73. Bolker B, Holyoak M, Krivan V, Rowe L, Schmitz O. 2003 Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* **84**, 1101–1114. (doi:10.1890/0012-9658(2003)084[1101:CTAESO]2.0.CO;2)
74. Werner EE, Peacor SD. 2003 A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**, 1083–1100. (doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2)
75. Yamauchi A, Yamamura N. 2005 Effects of defense evolution and diet choice on population dynamics in a one-predator-two-prey system. *Ecology* **86**, 2513–2524. (doi:10.1890/04-1524)
76. Bergquist DC, Ward T, Cordes EE, McNelis T, Howlett S, Kosoff R, Hourdez S, Carney R, Fisher CR. 2003 Community structure of vestimentiferan-generated habitat islands from Gulf of Mexico cold seeps. *J. Exp. Mar. Biol. Ecol.* **289**, 197–222. (doi:10.1016/S0022-0981(03)00046-7)
77. Carney RS. 1994 Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. *Geo-Mar. Lett.* **14**, 149–159. (doi:10.1007/BF01203726)
78. Tunnicliffe V. 1991 The biology of hydrothermal vents: ecology and evolution. *Oceanogr. Mar. Biol.* **29**, 319–407.
79. MacAvoy SE, Morgan E, Carney RS, Macko SA. 2008 Chemoautotrophic production incorporated by heterotrophs in Gulf of Mexico hydrocarbon seeps: an examination of mobile benthic predators and seep residents. *J. Shellfish Res.* **27**, 153–161. (doi:10.2983/0730-8000(2008)27[153:CPIBHI]2.0.CO;2)
80. Cordes EE, Becker EL, Fisher CR. 2010 Temporal shift in nutrient input to cold-seep food webs revealed by stable-isotope signatures of associated communities. *Limnol. Oceanogr.* **55**, 2537–2548. (doi:10.4319/lo.2010.55.6.2537)
81. van der Heide T, Bouma TJ, van Nes EH, van de Koppel J, Scheffer M, Roelofs JGM, van Katwijk MM, Smolders AJP. 2010 Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem. *Ecology* **91**, 362–369. (doi:10.1890/08-1567.1)
82. Dearing MD, Foley WJ, McLean S. 2005 The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annu. Rev. Ecol. Evol. S* **36**, 169–189. (doi:10.1146/annurev.ecolsys.36.102003.152617)
83. Schmidt KA. 2000 Interactions between food chemistry and predation risk in fox squirrels. *Ecology* **81**, 2077–2085. (doi:10.1890/0012-9658(2000)081[2077:IBFCAP]2.0.CO;2)
84. Moore BD, Foley WJ. 2005 Tree use by koalas in a chemically complex landscape. *Nature* **435**, 488–490. (doi:10.1038/nature03551)
85. DeGabriel JL, Moore BD, Foley WJ, Johnson CN. 2009 The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. *Ecology* **90**, 711–719. (doi:10.1890/08-0940.1)
86. Saikkonen K, Faeth SH, Helander M, Sullivan TJ. 1998 Fungal endophytes: a continuum of interactions with host plants. *Annu. Rev. Ecol. Evol. S* **29**, 319–343. (doi:10.1146/annurev.ecolsys.29.1.319)
87. Verstraete B, Van Elst D, Steyn H, Van Wyk B, Lemaire B, Smets E, Dessein S. 2011 Endophytic bacteria in toxic South African plants: identification, phylogeny and possible involvement in gousiekte. *PLoS ONE* **6**, e19265. (doi:10.1371/journal.pone.0019265)